

STUDIES ON NORTH AMERICAN CARBONIFEROUS INSECTS 1. THE PROTODONATA¹

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Introduction

This is the first of a series of papers based upon insects from Carboniferous strata in North America. The studies will be concerned in the main with previously described specimens (mostly types) in the Museum of Comparative Zoology, the U. S. National Museum and the Peabody Museum at Yale University, but will include new material whenever it is available.

Order Protodonata

Up to the present time only three species of Protodonata have been described from North American deposits of Carboniferous age. The present paper includes the description of a fourth species and an account of the previously described ones. In addition, I have included a discussion of the status of the ordinal name Protodonata.

One of these protodonates belongs to the family Meganeuridae and another to the Paralogidae. The remaining two are best referred to *Incertae Sedis* for family designation, although their protodonate affinities are unquestionable.

Family Meganeuridae

Typus durhami, n. sp.

Plate 11; text figure 1.

Forewing: greatest length of preserved part, 88 mm.; estimated complete length, 175 mm.; maximum width of preserved part, 27 mm. The venational details of both fore and hind wings, so far as preserved, are shown in text figure 1. The general venational pattern is close to that of *permianus* and other known species of the genus. The cells of the wings are larger than those of *permianus*, especially in the area between MA and CuP; R₂+3 and R₄+5 seem to diverge even more gradually in *durhami* than in *permianus*. The basal origin of

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R₃ is not preserved in the fore wing but in the hind wing it is clearly visible and is associated with the oblique cross-vein (Sn) characteristic of most Meganeuridae (Carpenter, 1947, p. 47); the cross-vein is not so pronounced as it is in *permanus*, however. The differences between the fore and hind wings in the proximal region are like those in other species of *Typus*.

Holotype: U. S. National Museum, Washington, D. C.² The specimen (field number 8758) was collected in May, 1939, by Mr. Charles B. Read at Durham, Georgia, the locality data being "Catoosa (TVA. Durham Quad.), Williams Coal Company Mine in No. 4 Coal. Plants from roof shale." According to Butts' account of the stratigraphy of the Paleozoic area in northwest Georgia (Butts and Gildersleeve, 1948, pp. 54-56), the coal mines at Durham are in the Walden sandstone part of the Pottsville Series. Butts states that "according to the best knowledge, the Pottsville Series of Georgia is of Lower Pottsville age and falls within the limits of the Lee Conglomerate of Tennessee and Virginia and corresponds approximately to the lower part of the Pottsville of the anthracite coal fields of Pennsylvania which carry the Lykens number 4 and 5 and the Lykens Valley coals." A brief discussion of the nature of the no. 4 coal at Durham is contained in Gildersleeve's account (*ibid.*, 1948, p. 104) of the mineral resources of the Paleozoic area in northwest Georgia.

As can be seen from the photograph (Plate 11), the specimen consists of the apical portions of the fore and hind wings; although the remainder of the insect, which was presumably originally preserved, is broken away, the preserved portions are very clear. I have assigned this species to the genus *Typus* but it might conceivably belong to *Megatypus* or *Boltonites*; the absence of the basal part of the wing containing the regions of the anal crossing and the second anal vein prevents a more definite generic assignment.

The interest attached to this species is in the evidence which it provides for the existence of the Meganeuridae in North America during the Carboniferous. It is the first such fossil that can be definitely assigned to the family. Furthermore, *Typus durhami*, occurring in the Lower Pottsville Series (corresponding approximately to Westphalian A), is among the oldest fossil insects known from North America.

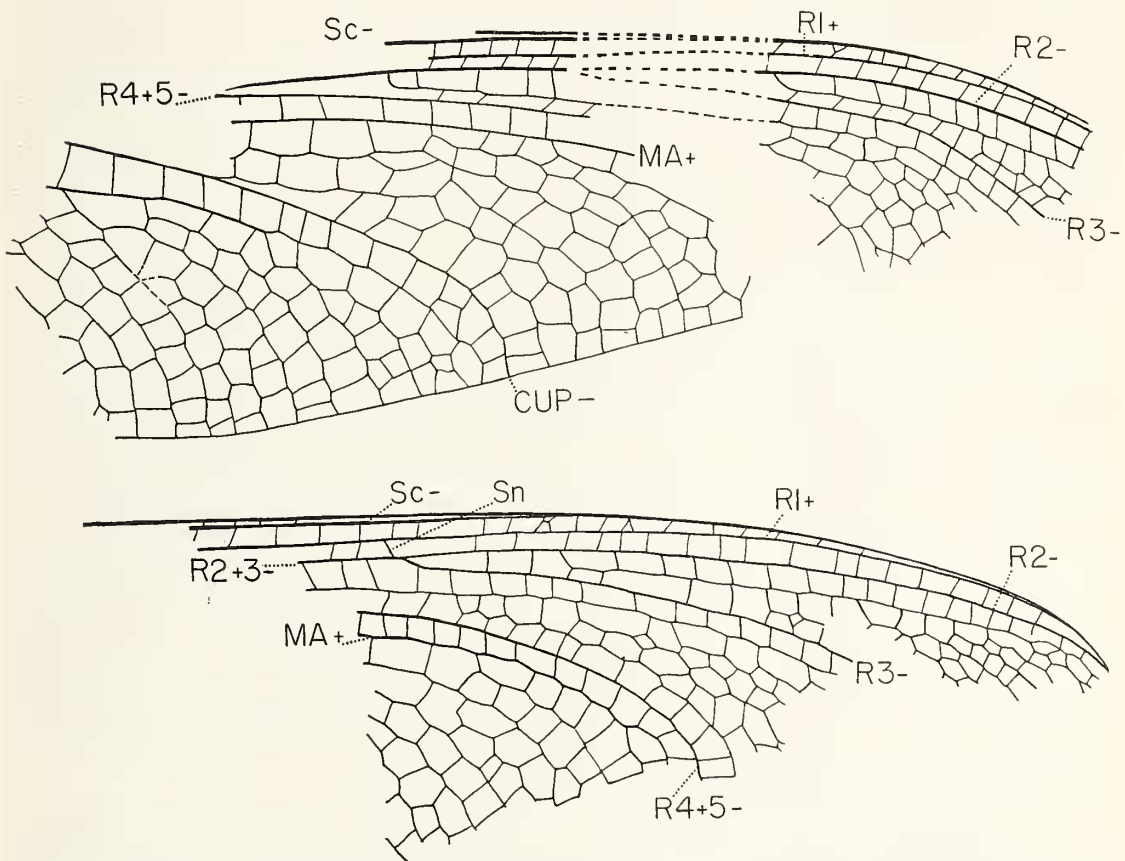
²I am indebted to Dr. S. H. Mamay of the United States Geological Survey for sending me this specimen for study.



CARPENTER — PROTODONATA

Family Paralogidae

The distinctive features of this family are the short subcosta, which terminates just beyond the middle of the wing; and the widely divergent branches of Rs ($R_2 + 3$ and $R_4 + 5$). The complete absence of the apparent vestige of CuA may also be a family trait. *Paralogus* is the only Carboniferous genus that clearly belongs here but in my opinion the Permian genus *Oligotypus* Carp. does also. Fraser (1957) considered *Oligotypus* to be a meganeurid, but, as shown below, his concept of the Paralogidae has not been entirely correct. *Oligotypus*



Text figure 1. Drawing of *Typus durhami*, n. sp. (holotype), fore and hind wings. Sc, subcosta; Rs, radius; R_2 , R_3 , $R_4 + 5$, branches of radial sector; MA, anterior media; CuP, posterior cubitus; Sn, subnodal vein.

differs from *Paralogus* only in minor details: the wing is somewhat more slender, and the branches of MA and 1A arise as a series of irregular veinlets, instead of distinct branches as in *Paralogus*. The following review of the structure of *Paralogus* strengthens my conviction that it and *Oligotypus* belong to the same family.

EXPLANATION OF PLATE 11

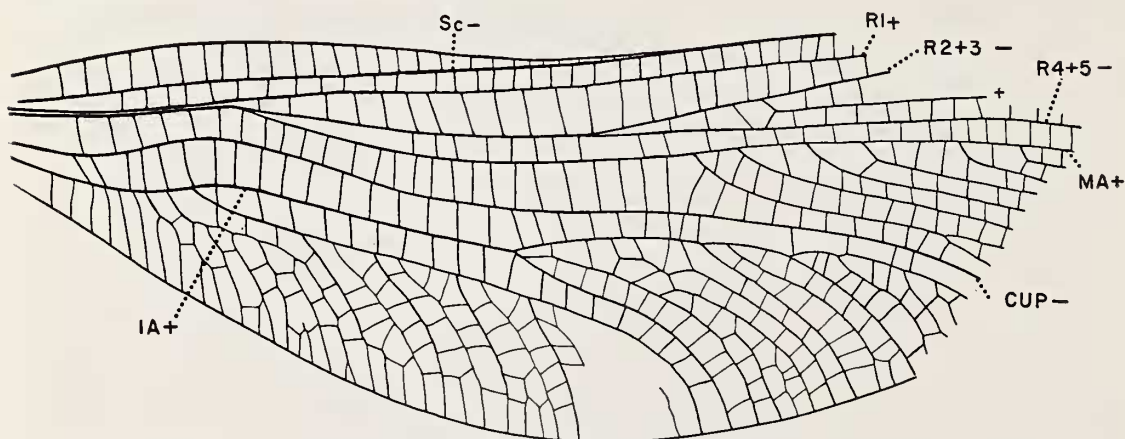
Photograph of *Typus durhami*, n. sp. (holotype) $\times 11/10$.

Paralogus aeschnoides Scudder

Text figure 2.

Paralogus aeschnoides Scudder, 1893, U. S. Geol. Surv., Bull. 101: 21; pl. 1, fig. a.

The unique specimen on which this species was based was collected by Mr. F. P. Gorham (1889) in Upper Carboniferous rocks at Silver Spring, East Providence, Rhode Island, and was donated to the Museum of Comparative Zoology by Professor Gorham in 1932. It consists of a well-preserved wing, about two-thirds complete. Scudder's drawing of the fossil is good and even shows by means of shading the convexity and concavity of the veins. I have included here a new description and an original illustration of the fossil, in part because a few details of phylogenetic significance were not clearly indicated by Scudder and in part because Dr. Fraser's recent illustration of the fossil (presumably based on Scudder's drawing) is misleading in several important respects.



Text figure 2. Drawing of *Paralogus aeschnoides* Scudder (holotype). Lettering as in text figure 1.

The wing fragment, as preserved, is 54 mm. long, and has a maximum width of 19 mm.; the complete wing was probably about 80 mm. long. The subcosta terminates a short distance beyond the middle of the wing and beyond the point of separation of $R_2 + 3$ and $R_4 + 5$. The two latter veins diverge widely after their origin; MA has a series of pectinate branches beginning just beyond the divergence of $R_2 + 3$ and $R_4 + 5$; just before the level of this divergence, IA separates into a divergent fork and sends a series of additional branches towards the distal part of the wing.

The wing itself is broad for a protodonate and has a strongly curved posterior margin. However, on the basis of our knowledge of the differences between the fore and hind wings of Meganeuridae, I

believe that the specimen of *aeschnoides* is a fore wing. At any rate, the distance between the posterior margin of the wing and the first anal is like that of other protodonate fore wings, not hind wings.

As can be seen from Scudder's illustration, the wing was subjected to some distortion in the process of preservation; it rests on a very uneven surface of the rock, so that the contour of the anterior margin of the wing is difficult to follow exactly. This is made worse by the presence of a slight "fault" extending obliquely across the wing, so that the veins in the anterior part of the wing are not quite aligned on the two sides of the fault. The result of the faulting and of the irregularity of the surface of the rock is to cause a more pronounced curvature of the anterior margin of the wing than would presumably otherwise have been present. The drawing in text figure 2 has been made without any attempt to restore the presumed original shape of the wing, apart from aligning the veins across the fault.

Scudder's representation of the shape of the wing is correct, the proportions of his drawing being approximately the same as those in the fossil. On the other hand, Fraser's drawing (1957, figure 11), showing a markedly broad wing and strongly curved posterior margin, is apparently incorrect. At any rate, I do not know of any evidence which supports this conception of the wing. Two other, more minor, corrections in Fraser's figure should be noted. The vein which he has labelled R₃ is a convex intercalary vein; R₂ and R₃ presumably separate much further along the wing. Also, the subcosta terminates gradually somewhat beyond the level of the separation of R₂ + 3 and R₄ + 5, not abruptly before this level as shown in Fraser's drawing. The short basal vein, termed CuA, which is consistently present in the meganeurids, is not discernible in the specimen of *aeschnoides* although Dr. Fraser has shown it in his drawing. The absence of this vein appears to be another characteristic shared by *Paralogus* and *Oligotypus*.

The deposit in which the specimen of *aeschnoides* was found is usually referred to the Allegheny or Conemaugh Series, about equivalent to the Upper Westphalian of Europe.

Family: Incertae Sedis

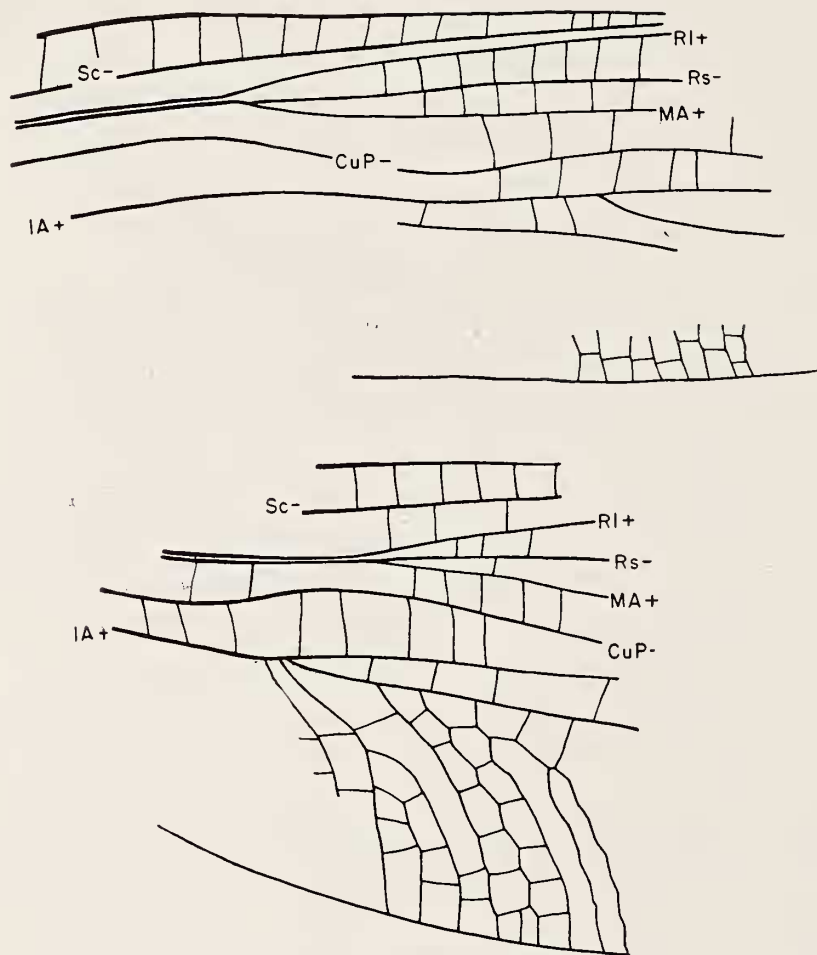
Paralogopsis longipes Handl.

Text figure 3.

Paralogopsis longipes Handl., 1911, Amer. Journ. Sci., (4) 31: 374, fig. 58.

The specimen on which this species was based is contained in an ironstone nodule from the vicinity of Mazon Creek, Illinois; the type

is in the Peabody Museum at Yale University, where I examined it several years ago. Although Handlirsch figured only the hind wing (so far as it was preserved), a portion of the fore wing is also present; this is clearly narrow, more like that of the Meganeuridae than of the Paralogidae, where *Paralogopsis* has previously been placed (Fraser, 1957). However, since the key parts of the wings (such as the forking of Rs) are not included in the preserved portion, the family relationships remain obscure.



Text figure 3. Drawing of *Paralogopsis longipes* Handl. (holotype). Lettering as in text figure 1.

The significance of this fossil is that it provides the only record of the Protodonata in the Carboniferous strata of the Eastern Interior Region of North America. The Frances Creek shales, which yield these ironstone nodules, are considered part of the Carbondale Formation; this is regarded as about equivalent to the middle or late Westphalian stage (late C or early D) of Europe.

Palaeotherates pennsylvanicus Handl.

Text figure 4.

Palaeotherates pennsylvanicus Handlirsch, 1906, Proc. U. S. Nat. Mus., 29: 690, fig. 17.

Palaeotherates pensilvanicus [sic] Handlirsch, 1906, Fossilen Insekten: 311; pl. 32, fig. 5.

The fossil on which this species was established consists of a wing fragment preserved in black shale; it was collected in 1887 in interconglomerates, at Coxtton, one mile north of Pittston, Pennsylvania. The type specimen, which is in the U. S. National Museum (No. 38787), was kindly loaned to me for study through the courtesy of Dr. G. A. Cooper.

Handlirsch's drawing of the fossil, although correctly representing the general venational features, omitted two significant details, — the subnodal vein and the costa. He recognized that the "second vein" must be the radius (R1), but since he could detect no anterior vein, other than a marginal one, he concluded that the subcosta had fused with the costa in the area of the wing preserved. However, the clear preservation of the subnodus (Sn), which Handlirsch did not figure, shows that the part of the wing represented was too near the middle of the wing for the termination of the subcosta to have taken place. Furthermore, careful study of the fossil shows that the anterior margin of the wing (costa) is actually present as distinct from the subcosta in the distal part of the fossil, although it is broken away along the rest of the wing fragment. It now becomes clear that the fossil represents a fragment of the wing just beyond the middle; it includes the point of separation of R2 and R3, but not the separation of R2 + 3 and R4 + 5. Handlirsch's naming of the veins is incorrect; the convexities and concavities, which are clearly preserved in the fossil, show that R4 + 5 was included in the complex which he termed the media.

The original insect was probably about the size of most species of *Typus*, not "very large" as estimated by Handlirsch. The wing fragment is 45 mm. long, and on the basis of comparisons with other protodonates, it probably represents about one-third of the complete wing. Since the width of the wing of *pennsylvanicus* is 18 mm., its original dimensions were probably close to those of *Typus gracilis* Carp. (Permian), which is 145 mm. long and 26 mm. wide.

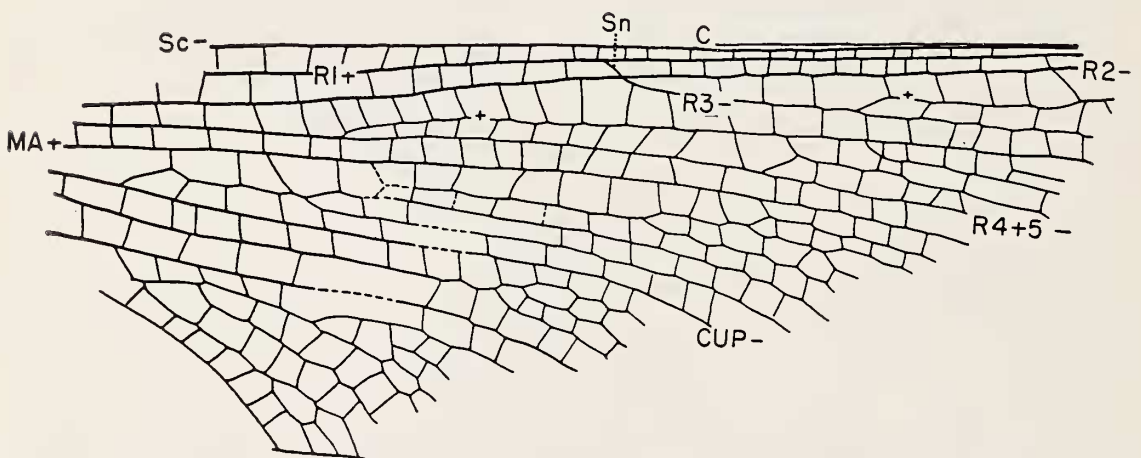
The drawing of the fossil shown in text figure 4 is based on the type specimen. The venational pattern, so far as it is known, is like

that of the meganeurids, but, since the proximal half of the wing is unknown, I consider the family position uncertain. It is clearly not a member of the Paralogidae, where it was placed by Fraser (1957).

The deposit in which this fossil was collected appears to be of upper Pottsville age corresponding to Westphalian C of the European classification.

Status of the Ordinal Name Protodonata

I take this opportunity to discuss the status of the ordinal name Protodonata, in an attempt to clear up some of the confusion which has appeared in the literature in recent years. Handlirsch (1906b) first defined this group as an order in 1906³ and he placed here three new



Text figure 4. Drawing of *Palaeotherates pennsylvanicus* Handl. (holotype). Lettering as in text figure 1.

³Much confusion has resulted from two, almost simultaneously published works by Handlirsch, both appearing in 1906. His *Revision of American Paleozoic Insects* (Proceedings of the U. S. National Museum, Vol. 29, pp. 661-820) is an English translation of a specially prepared account of the Paleozoic insects then known from North American deposits. New species, genera and higher taxa were described and illustrated. His *Die Fossilen Insekten* was published by Englemann in Leipzig in parts over a period of two years. The first part, consisting of pages 1-640, was published in 1906 (See *Fossilium Catalogus*, (I), Pars 16, 1922, p. 10). This part dealt with the Paleozoic insects and included, among the others, descriptions and figures of the North American fossils. That this work was published *after* the English account is shown by the references in *Die Fossilen Insekten* to specific pages in the Proceedings article. Unfortunately, many (but not all) of the species, genera and higher taxa already described in the Proceedings account were described again and designated as new in the larger, German treatise.

In reality, the first designation of the Protodonata as an *order* was made in the Proceedings article mentioned above. The discussion of the characteristics of the order was essentially that given later in *Die Fossilen Insekten*, but only two genera, *Paralogus* and *Palaeotherates*, were actually mentioned as included in the order.

families: Protagrionidae Handl., Meganeuridae Handl., and Paralogiidae Handl. The Protagrionidae⁴ were known only from a single wing (*Protagrion audouini*), but the Meganeuridae were known from many specimens, some of which included the body structures. Handlirsch's definition of the order was accordingly based on the meganeurids and the order itself was considered by him to be related to both the Paleodictyoptera and the Odonata. In the course of several years, as more meganeurids and Paleodictyoptera were found, it became increasingly evident that the Protagrionidae were not at all closely related to the Meganeuridae or to the Odonata. In 1932, Martynov (1932a), after pointing out the differences between these two groups, removed the Meganeuridae and Paralogiidae from the Order Protodonata and placed them in a new order which he erected for them, the Meganisoptera. The Order Protodonata was therefore left with the family Protagrionidae, which was then recognized as having no odonate affinities.

In 1943, after a detailed study of the original specimen of *Protagrion audouini* (preserved in the Paris Museum), I published an account of this fossil and transferred the family Protagrionidae to the Paleodictyoptera, where it clearly belongs, in association with several related families; at the same time I restored the Meganeuridae and Paralogiidae to the Order Protodonata, as they were originally placed by Handlirsch.

In 1957, in his account of the classification of the Odonata (p. 21), Fraser agreed to the separation of the Protagrionidae from the Meganeuridae and Paralogiidae, but he insisted that the name Protodonata must be associated with *Protagrion*, and contended that I was in error in placing the Meganeuridae in the Order Protodonata. His reason for these assertions was that "Brongniart established his family Protagriidae [Protagrionidae] on a single genus *Protagrion* (1885); the family was therefore a monotypic one and by the International Rules of Nomenclature it matters not whether the family afterwards assumed ordinal rank or that further genera or families were added to it, it must take the characters from *Protagrion*, that is, from the original type."

⁴Throughout this article I am using the name Protagrionidae, instead of Protagriidae, for the family based upon the genus *Protagrion*. This is in accordance with the information provided by Professor Joshua Whatmough of Harvard University and published in B. E. Montgomery's article on this subject (*Annals Ent. Soc. Amer.*, 47: 473-474, 1954).

It is clear from this quoted passage that Fraser's conclusions are based on his belief that *Protagrion* was designated by Brongniart as the type genus of the Order Protodonata and that the Rules of Nomenclature consequently require us to use that conception of the order. I believe it is Dr. Fraser who is in error here. The Rules of Nomenclature have not been applied by the Commission on Nomenclature to orders and higher taxa. The accepted policy regarding these higher categories has been well summarized by Simpson in his recent discussion of the principles of taxonomy (1961, p. 30): "Proposals have been made to extend the type system (and priority) to names of still higher taxa, above superfamilies, but this provision is not now embodied in the Rules or in general usage. At present the names of those higher taxa, of course much less numerous than names of genera or species, are determined only by consensus and acceptance of authority, and at these levels that informal system seems to work at least as well as the Rules do at lower levels."

Since the term Protodonata was first used in an ordinal capacity by Handlirsch (1906b), as I have stated above, and since his definition of the order was based mainly on the Meganeuridae, I prefer to use the name Protodonata for the order containing the Meganeuridae.

Moreover, if the Rules of Nomenclature are applied to the ordinal name here, I contend that *Protagrion* has no standing as the type genus of the Protodonata and that, in fact, the genus *Meganeura* more logically and appropriately stands as the type genus. In this connection it is necessary to correct Fraser's statement quoted above, that "Brongniart established his family Protagriidae on a single genus *Protagrion* (1885)". At no time did Brongniart ever use the family name Protagriidae [Protagrionidae]; it was first used by Handlirsch in 1906 (1906b). Consequently, this statement by Fraser has no meaning or application whatsoever to the term Protodonata. The name Protodonata was first used by Brongniart in 1885 (p. 55). In this paper Brongniart discussed a series of orders, one of these being the "Neurorthopteres" and another the "Pseudoneuroptera". In this latter order he placed, among others, two families, one which he called Megasecopterida and another which he designated Protodonata. His precise statement about the "family Protodonata" is as follows: "Je rangerai à côté de ces Megasecopterida un type ancestral des Libellules; la création de la famille des Protodonata . . . et du genre *Protagrion* . . . me semble nécessaire. Une aile seulement a été trouvée jusqu'ici à Commentry; elles [sic] mesure 10 centimètres de

long et 2 centimètres de large. Sa forme, sa nervation et sa réticulation rappellent beaucoup celle des Odonates actuels. Il y a cependant d'assez notables différences."

Since this was the first mention of the genus *Protagrion* in the literature anywhere and since there was no mention of any species in the genus, the name *Protagrion* was a *nomen nudum*. This use of the term Protodonata did not, therefore, establish a precedent or policy with respect to use of the name. The next use of the term Protodonata, again for a family, was by Brongniart in 1894 (p. 394). At the beginning of Chapter V, entitled "Protodonata", there was a discussion of the characteristics of the Protodonata based almost entirely on *Meganeura*; the genus *Protagrion* was not even mentioned there. In the descriptive part of the work, the first genus considered was *Meganeura*, which was fully described, along with two species in the genus, *monyi* and *selysii*. The other genera also assigned in the "family Protodonata" in chronological order were: *Paralogus*, *Titanophasma*, *Protagrion*, *Campyloptera*, and *Brodia*. *Protagrion* was, therefore, fourth in the series of genera placed in the "family Protodonata". From this I think it is clear that there is no basis for Dr. Fraser's statement that the Order Protodonata "must take the characters of *Protagrion*".

Since the first definition of the Protodonata as an order (Handlirsch, 1906b) was based mainly on the Meganeuridae, and since Brongniart's first valid use (1894) of the term Protodonata for a "family" was based almost exclusively on *Meganeura*, I do not accept the removal of the Meganeuridae from the Protodonata and the erection of another order (Meganisoptera) for that family. In my opinion the Order Meganisoptera is identical with the Order Protodonata.

Whether the Protodonata should be considered a separate order or a suborder of the Odonata is largely a matter of personal choice. Fraser (1957, p. 24) considers the group (Meganisoptera) to be a suborder, whereas Martynov (1932b, p. 43; 1938, p. 62) treated it as a distinct order. I strongly support its ordinal rank; the absence of a nodus, a pterostigma and a true arculus places these insects outside the phylogenetic complex of the Odonata.

REFERENCES

- BRONGNIART, C. 1885. Les insectes fossiles des terrains primaires. Bull. Société Amis des Sciences Naturelles de Rouen, 1885: 50-68.
1894. Recherches pour servir à l'histoire des insectes fossiles des temps premaières. Saint-Etienne (1893), pp. 1-493.
- BUTTS, C. and B. GILDERSLEEVE 1948. Geology and mineral resources of the Paleozoic area in northwest Georgia. Georgia Geol. Surv., Bull. 54: 1-176.
- CARPENTER, F. M. 1943. Studies on Carboniferous insects from Commeny, France, Part 1. Geol. Soc. Amer., Bull. 54: 527-554.
1947. Lower Permian insects from Oklahoma.. Part 1. Proc. Amer. Acad. Arts and Sci., 76: 25-54.
- FRASER, F. C. 1957. A reclassification of the Order Odonata. Royal Zool. Soc. New South Wales. Pp. 1-133.
- HANDLIRSCH, A. 1906a. Revision of American Paleozoic insects. U. S. Nat. Mus., Proc., 29: 661-820.
1906b. Die Fossilen Insekten. Leipzig, pp. 304-311.
1911. New Paleozoic insects from the vicinity of Mazon Creek, Illinois. Amer. Journ. Sci. (4) 31: 297-377.
- MARTYNOV, A. B. 1932a. New Permian Palaeoptera with the discussion of some problems of their evolution. Trav. Inst. Paleozool. Acad. Sci. 1: 1-44.
1932b. On the wing-venation in the family Meganeuridae (Meganisoptera). Compt. Rendus Acad. Sciences URSS, 1932: 42-44.
1938. Etudes sur l'histoire géologique et de phylogénie des ordres des insectes (Pterygota). Trav. Inst. Paleont., 7: 1-149.
- SCUDDER, S. H. 1893. Insect fauna of the Rhode Island coal field. U. S. Geol. Surv. Bull., 101: 1-21.
- SIMPSON, G. G. 1961. Principles of animal taxonomy. Columbia Univ. Press, pp. 1-247.